COMPARISON OF DEVELOPMENT IN DODDER AND MORNING GLORY[1]

GERTRUDE ELIZABETH MACPHERSON

(WITH PLATES XXV–XXVII)

The embryo of *Cuscuta Gronovii* Willd. is described in BRITTON and BROWN'S *Flora of the Northern United States and Canada* as follows: "Embryo linear, terete, curved or spiral, its apex bearing 1–4 minute scales; endosperm fleshy, cotyledons none." The purpose of this study was to determine whether there might not be at least a trace of cotyledonary development. In examining embryos of *Cuscuta*, which is a parasite, for indications of a rudimentary development of cotyledons, it seemed desirable to make a comparison with some non-parasitic species of the same family, and *Convolvulus sepium* L. was selected for this purpose.

By far the larger number of previous studies of *Cuscuta* have been concerned with the physiology of the plant, its host relationships, or geographical distribution, and few with the life history and morphology.[2] Miss HOOKER mentions the presence of scales on the inner and outer surface of the curve of the coiled embryo, but states that their position does not justify considering them cotyledons. The remainder of her paper discusses the habits of growth of *Cuscuta Gronovii*. COULTER and CHAMBERLAIN,[3] in discussing the endosperm, remark that, contrary to the usual course of development in parasites, the endosperm of *Cuscuta* is formed by free nuclear division, and later in treating of the types of embryos in Angiosperms they state that the embryo of *Cuscuta* is also an exception to the morphology of parasites in that it is large and well developed. These are the only important references to the embryo of *Cuscuta* that have come to the writer's attention.

[1] Paper no. 14 of the technical series, New Jersey Agricultural Experiment Station, department of plant pathology.

[2] HOOKER, HENRIETTA E., On *Cuscuta Gronovii*. BOT. GAZ. **14**:31–37. 1899.

[3] COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. Chicago. 1903 (pp. 174, 176).

The material was collected in September. The *Cuscuta* material was killed, part in a chromo-acetic solution and part in a picro-acetic solution, and the germinated seeds in a fixing solution consisting of 60 cc. of 95 per cent alcohol, 35 cc. of water, 5 cc. of formaldehyde, and 2 cc. of glacial acetic acid. All the *Convolvulus* material was killed in this latter fixing solution. The *Cuscuta* and *Convolvulus* were treated in the usual way and imbedded in paraffine, sectioned, and stained, some in haematoxylin, some in haematoxylin and eosin, and the larger part in iron-alum haematoxylin. The sections of *Cuscuta* were cut about 25 μ in thickness and those of *Convolvulus* about 10 μ in thickness.

The ovule in both species is anatropous (figs. 1, 20). The development of the embryo sac up to and including the 8-celled stage both for *Cuscuta* and *Convolvulus* follows the usual method. In the 2-celled stage of the embryo sac of *Cuscuta Gronovii* (fig. 2) there is a dense mass of protoplasm lying between and surrounding the two nuclei which are located at the ends of the sac. In the 4-celled stage (fig. 3) the sac is much larger and the protoplasm less dense. In the 8-celled stage (fig. 4) the sac is somewhat larger, and the protoplasm is most abundant immediately surrounding the polar nuclei. The synergids and egg are large, prominent, and somewhat irregular, but conform to the usual type. The antipodals are much smaller, but very distinct and well defined. The polars are oval, intermediate in size between those of the egg apparatus and the antipodals, and vacuolate. At this time the cells of the nucellus show the presence of a large quantity of starch grains (fig. 4), which, on account of their taking the stain so much more readily, render the nucellus very conspicuous. The cells of the nucellus are rich in starch, and those immediately surrounding the embryo sac show indications of rapid disintegration, accompanying the enlargement of the sac.

As previously stated, COULTER and CHAMBERLAIN describe the endosperm of *Cuscuta* as arising by free nuclear divisions and not by continuation of the process of cell division, with the formation of walls. This is contrary to the usual course of development of the endosperm in saprophytic and parasitic dicotyledonous

species. In most saprophytic and parasitic dicotyledonous plants the first division of the endosperm nucleus is accompanied by the formation of a wall which divides the sac into two chambers; but this is not true in *Cuscuta Gronovii*. The endosperm at all times is rather scanty, and this is especially true in the mature seed. The cells of the endosperm are elongated, with more or less elliptical nuclei, and are most frequently seen clustered around the embryo, rather than lining the sac as in *Piper medium*, *Potomageton* sp., etc. (figs. 18, 19).

The youngest embryo observed in *Cuscuta* was a 2-celled stage (fig. 5). It was spherical, and the basal cell was larger than the apical cell, both cells showing large, well defined nuclei. The two cells were evidently formed by transverse division of the fertilized egg. The later stages (figs. 5–7) appear to be the result of division in a number of planes and in no fixed order, resulting in embryos of irregular forms. The most usual form is an elongated type with a swollen base (fig. 8), having a suspensor of one cell, or no suspensor. There is a spherical type (figs. 9, 10) which is much less common. In later stages of development both spherical and elongated forms are found, in some cases with a 2-celled suspensor (figs. 11, 12), but more often with none. In neither spherical nor elongated forms is there any differentiation into dermatogen, nor later is there any indication of plerome or periblem. In some of the embryos where the shape is rather urnlike, the swollen base is formed by lateral enlargements (figs. 13, 14), but these cannot be an indication of cotyledons, for the cells of which they are formed are not differentiated in any manner from the rest of the embryonic tissue. Both the spherical and urnlike embryos continue to elongate (fig. 15) without any trace of differentiation, and finally form a long coiled embryo (fig. 16), large and well developed, and consisting of about two spirals, lying in the rather scant endosperm of the mature seed. The embryo of the mature seed bears two small scales near the apex (fig. 17*a* and *b*), one on the inner surface of the coil and the other slightly below this on the outer surface. Neither of these scales, however, from their relation to the other parts of the embryo, can be considered as cotyledons.

The stages in the embryo sac of *Convolvulus* are virtually the same, but smaller than in *Cuscuta Gronovii* (fig. 21). In the 8-celled stage the protoplasm is more dense than that occupying a similar position in the 8-celled sac of *Cuscuta Gronovii*. The synergids and egg do not differ much in size as in *Cuscuta*. The polar nuclei and antipodals are of similar appearance, but the polar nuclei usually stand out more prominently than the other nuclei. Here also the nucellar cells show evidence of degenerating rapidly. Starch grains are present in these cells, but not in the quantities in which they are found in *Cuscuta*.

The difference in the position of the nuclei in the sac is the most noticeable feature. In *Cuscuta* the nuclei extend from one end of the sac to the other, with protoplasmic connections between, while in *Convolvulus* the nuclei are gathered nearer the micropylar end of the sac, where the protoplasm is aggregated. The first division of the fertilized egg in *Convolvulus sepium* was transverse (figs. 22*b*, 23), and resulted in the formation of an embryo very similar to that of *Cuscuta Gronovii*. The 4- and 8-celled stages (figs. 24, 25) were elongated and somewhat irregular in form, and much the same as in *Cuscuta*, but never exhibited the pronounced urnlike form. In stages of more than eight cells the embryo of *Convolvulus* is spherical (figs. 27, 29) in form, with a rather pronounced dermatogen in the majority of cases (figs. 28, 29). The embryo continues its growth until in the mature seed it appears surrounded by scant endosperm, the two large cotyledons folded around the hypocotyl (fig. 30). No stages of the embryo intermediate between those of the period of development of fig. 29 and the mature seeds were studied, but these indicate that the differentiation into tissues must have been in accord with the stages of normal embryonic development. In these advanced stages there is a very large suspensor (fig. 27) consisting of large, very vacuolated, uninucleate cells, which completely fill the micropylar end of the sac and force the embryo well out into the sac. The enormous development of the suspensor is much more rapid than that of the rest of the embryo, from which its separation is not always definite. There is also more endosperm than in the corresponding stage of *Cuscuta*. The endosperm forms

more of a lining for the sac than in *Cuscuta*, and is also associated with abundant perisperm in a number of cases (figs. 26, 31). The entrance of the pollen tube through the micropyle can easily be traced in *Convolvulus*, although it is not apparent in *Cuscuta*. The pollen tube remains in *Convolvulus* (fig. 32*a* and *b*) as late as the 4-celled stage of the embryo or later, apparently without being ruptured. The actual fusion of the tube and egg nucleus was not observed.

One of the striking points about the embryo of *Convolvulus* is the frequent occurrence of polyembryony. In *Cuscuta* not one case was observed, but in *Convolvulus* it soon became evident that polyembryony was not the exception to the rule, but a usual occurrence in the development of the embryo. Polyembryony may be observed from the earliest stages until quite a highly developed embryo is present. In one case several embryos were lying in the micropylar end of the sac, two of them consisting of two cells with a 1-celled embryo also present (fig. 22*a* and *b*), and 8-celled stages with one or more 1- or 2-celled embryos present were frequently observed (fig. 25), as were larger embryos that had the dermatogen developed (fig. 26). These extra embryos never developed at the antipodal end of the sac, and do not appear to be formed by the budding off from the fertilized egg. They seem rather to be formed from the synergids, or it may be that some of what appear to be 1-celled embryos are rather persistent synergids that have not developed any further and have not been absorbed. There may be some basis for assuming that polyembryony is the result of parthenogenesis.

Summary

1. Except for the enlargements of undifferentiated tissue on the sides of some of the embryos of *Cuscuta*, there appears to be no cotyledonary development.

2. The development of a large vacuolate suspensor is typical of the older embryos of *Convolvulus*.

3. Polyembryony is the rule rather than the exception in the development of the embryos of *Convolvulus*.

4. Multiple embryos in *Convolvulus* seem to be developed from the synergids.

5. The endosperm in *Cuscuta* is scanty, and in both *Convolvulus* and *Cuscuta* is the result of free nuclear division.

The writer wishes to thank Dr. MEL. T. COOK for suggesting this problem, and for his interest and assistance throughout the course of the investigation.

RUTGERS COLLEGE
NEW BRUNSWICK, N.J.

EXPLANATION OF PLATES XXV-XXVII

PLATE XXV

FIG. 1.—Longitudinal section of flower of *Cuscuta Gronovii*, showing position of ovule.

FIG. 2.—Longitudinal section of *Cuscuta Gronovii*, showing 2-nucleate stage of embryo sac.

FIG. 3.—Four-nucleate stage of embryo sac.

FIG. 4.—Eight-nucleate stage of embryo sac before mature organization, showing degenerating cells of nucellus, rendered prominent by presence of large number of starch grains.

FIG. 5.—Two-celled embryo.

FIG. 6.—Four-celled embryo with suspensor.

FIG. 7.—Eight-celled embryo, elongated type with swollen base.

FIG. 8.—Older embryos, same type as fig. 7.

FIG. 9.—Embryo of more spherical type.

FIG. 10.—Advanced embryo of elongated form.

FIG. 11.—Advanced embryo of spherical form with 2-celled suspensor.

FIG. 12.—Same type of embryo as fig. 11.

PLATE XXVI

FIG. 13.—Advanced embryo of urnlike form.

FIG. 14.—Urnlike embryo slightly older than fig. 13.

FIG. 15.—Very advanced embryo, showing elongation not accompanied by differentiation of embryonic tissue.

FIG. 16.—Coiled embryo as found in mature seed.

FIG. 17.—Apex of embryo showing two scales (*a*); apex of embryo showing structure of scale (*b*).

FIG. 18.—Endosperm in *Cuscuta* surrounding embryo rather closely.

FIG. 19.—Perisperm sometimes seen accompanying endosperm in *Cuscuta*.

FIG. 20.—Longitudinal section of *Convolvulus sepium*, showing type of ovule.

FIG. 21.—Eight-nucleate stage of embryo sac.

PLATE XXVII

FIG. 22.—Sac showing polyembryonic condition, containing 1- and 2-celled embryos (*a*); 1- and 2-celled embryos (*b*).

FIG. 23.—Two-celled embryo.

FIG. 24.—Four-celled embryo.

FIG. 25.—Older embryo and smaller one.

FIG. 26.—Older embryo with several 1- and 2-celled embryos, accompanied by abundant perisperm.

FIG. 27.—Young spherical embryo with suspensor of many vacuolate cells.

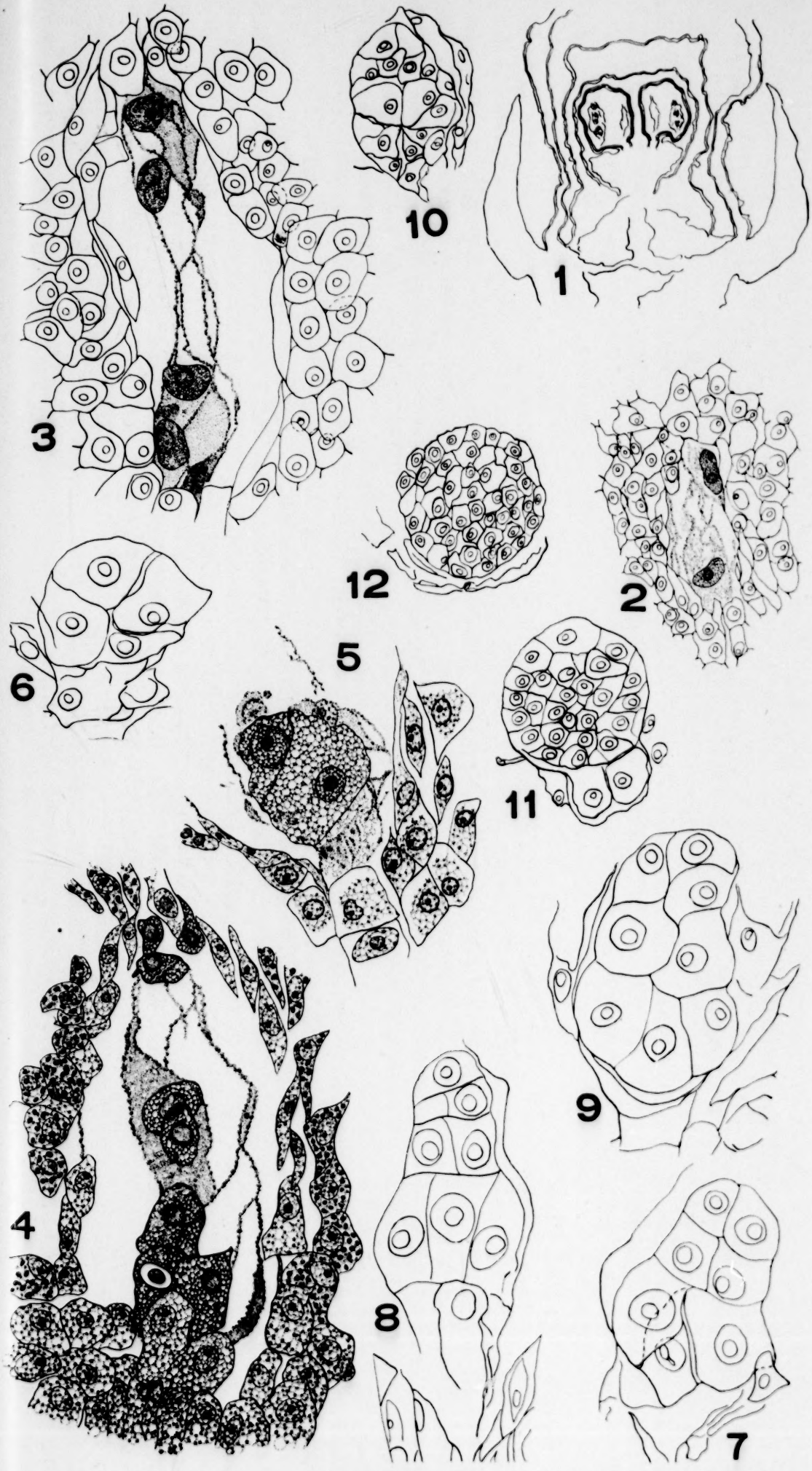
FIG. 28.—Older embryo and suspensor.

FIG. 29.—Advanced embryo of spherical type.

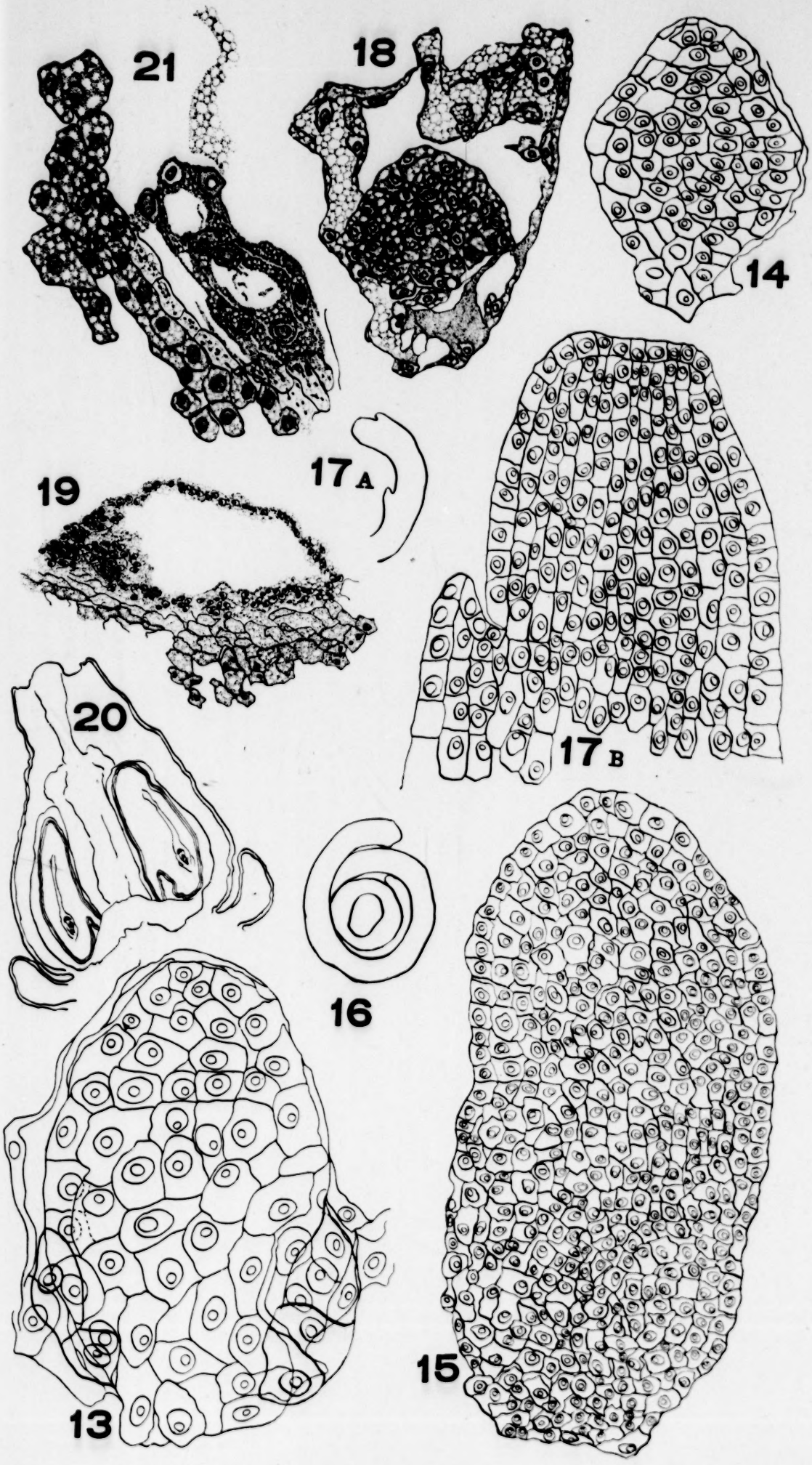
FIG. 30.—Embryo as found in mature seed, showing cotyledons and hypocotyl.

FIG. 31.—Endosperm in *Convolvulus* lying next to nucellus rather than close to embryo.

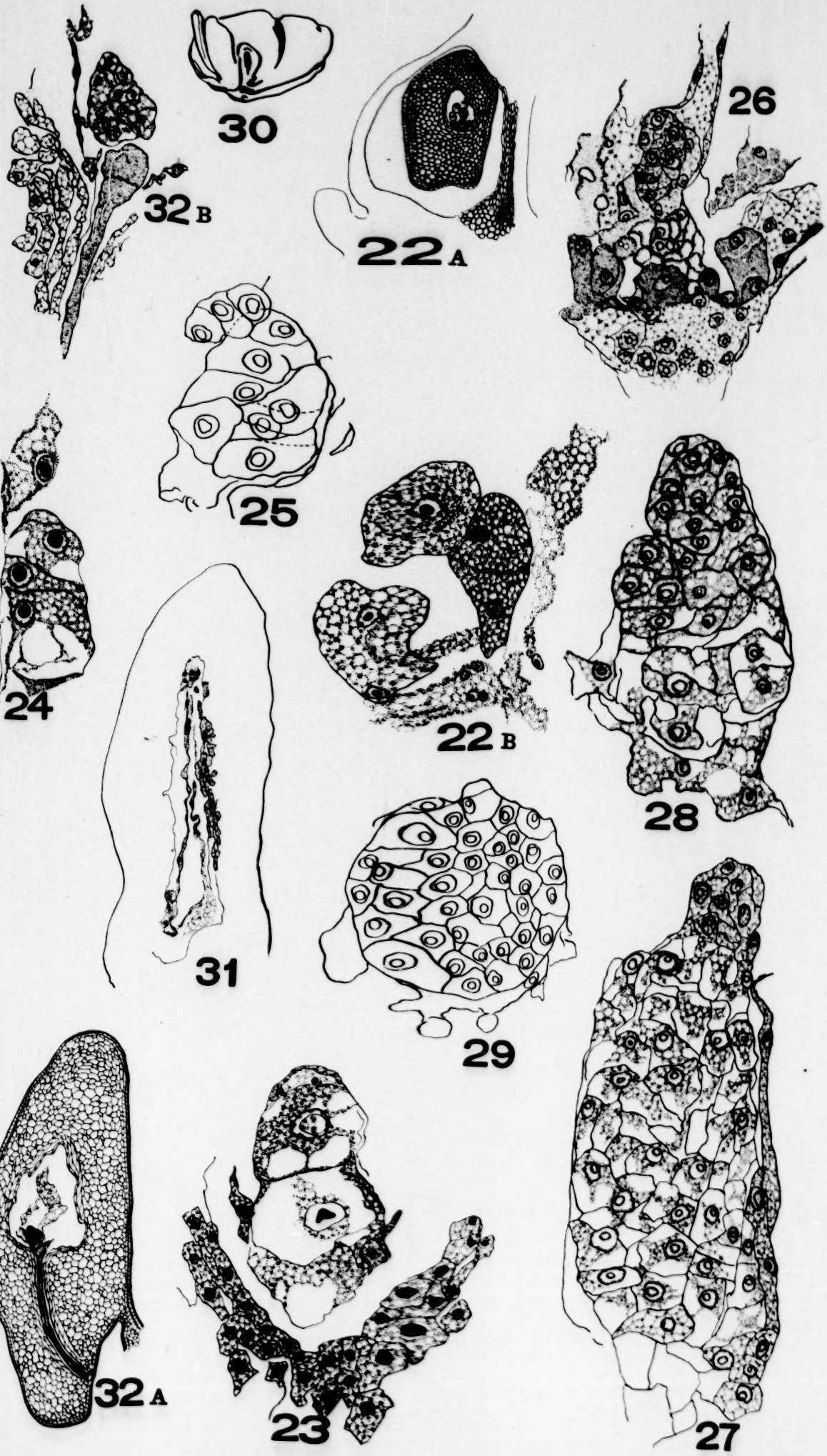
FIG. 32.—Sac containing many-celled embryo, showing entrance of pollen tube and inflated tip, with no indications of rupturing (*a*); same view showing micropylar end of sac (*b*).



MACPHERSON on CUSCUTA and CONVOLVULUS



MACPHERSON on CUSCUTA and CONVOLVULUS



MACPHERSON on CUSCUTA and CONVOLVULUS